Numerical Taxonomy of Some Fern Species in the Genus *Thelypteris* Schmidel *sensu lato* in Thailand

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Thelypteris Schmidel s.l. is a genus of the Thelypteridaceae. It is comprised of about one thousand species that mostly occur in tropical and subtropical regions of the world. Up to now, the genera within the Thelypteridaceae have not been clearly classified due to different generic concepts held by pteridologists. Some authors treat all species in a single genus, whilst others segregate *Thelypteris* s.l. into two or more genera. *Thelypteris* s.l. is commonly found in various habitats throughout Thailand. Fifty one species have been reported and placed into two genera. In contrast, these same species would be classified into 16 genera according to Holttum's classification. In order to clarify this taxonomic inconsistency, 518 OTUs from 27 species were analysed using cluster and canonical discriminant analyses. A total of 21 quantitative and 11 qualitative characters were employed. In the cluster analysis, using only quantitative characters, the 518 OTUs could be separated into three taxa or genera, i.e. *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium* using an average taxonomic distance of 1.50. The same result was obtained when both quantitative and qualitative characters were used. Likewise, canonical discriminant analysis suggested that there were three groups within the genus *Thelypteris* s.l. The three groups/genera can be distinguished on the basis of scale width, angle of basal pinnae to rachis, number of annulus cells, spore height and spore diameter. In all, the results from these morphometric analyses support the segregation of *Thelypteris* s.l. into three genera, viz. *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium*.

Key words: *Thelypteris*, cluster analysis, canonical discriminant analysis

Introduction

Thelypteridaceae is one of the largest families of seedless vascular plants, comprising nearly a thousand species mostly in tropical and subtropical regions; less than 2% are found in temperate areas. Diagnostic characters of the family Thelypteridaceae include the possessing of two meristeles throughout the length of stipe (compared to many meristeles in Dryopteroid ferns) and the presence of acicular hairs on many parts of the frond. Spores are bilateral with a prominent perispore. Chromosome base numbers of Thelypteridaceae range from 27 to 36 (Mickel and Beitel, 1988). In contrast, those of its related groups, i.e. Dryopteroids and Athyrioids, have 40 and 41 chromosome base numbers, respectively.

Up to now, the Thelypteridaceae can not be clearly classified, so that some genera are included or excluded from this fern family due to different concepts of various pteridologists. So far, the treatment concerning the circumscription and relationships of the Thelypteroid ferns are those given by Christensen (1938), Copeland (1947), Ching (1963), Morton (1963), Iwatsuki (1964) and Holttum (1971). Some authors, for example Morton (1963) treated all species as a single genus, i.e. *Thelypteris* Schmidel, whilst the others segregated the genus *Thelypteris* s.l. into two to more genera, for example Christensen (1938), Copeland (1960), Ching (1963), Iwatsuki (1964) and Holttum (1971).

The Thelypteridaceae is commonly found throughout Thailand. Fifty one species have been reported and treated in two genera, viz. *Thelypteris* and *Meniscium* (Tagawa and Iwatsuki, 1988), while Boonkerd and Pollawatn (2000) proposed a segregation of *Thelypteris* s.l. into 14 genera. It can be seen that classification within the Thelypteridaceae so far is not clear and is waiting for re-investigation.

Methodology

1. *Specimen collections*

Complete specimens of *Thelypteris* species were collected from their natural habitats (Table 1). They were determined to species using the key to species in the Flora of Thailand (Tagawa and Iwatsuki, 1988). Corresponding taxa according to Holttum's classification (Holttum, 1971 and 1981) were also determined. Then they were confirmed by comparing with the voucher specimens deposited at BCU, BKF, E, L, P, and K (Herbarium abbreviations according to Holmgren and Holmgren (2005).

Table 1. Twenty seven taxa of *Thelypteris* s.l. used in multivariate analyses

No.	Botanical Name (Tagawa & Iwatsuki, 1988)	Corresponding taxa after Holttum (1971, 1981)
1.	*Meniscium proliferum* (Retz.) Sw.	*Ampelopteris prolifera* (Retz.) Copel.
2.	*Thelypteris arida* (D. Don) Morton	*Christella arida* (D. Don) Holttum
3.	*Thelypteris ciliata* (Wall. ex Benth.) Ching	*Trigonospora ciliata* (Wall. ex Benth.) Holttum
4.	*Thelypteris confluens* (Thunb.) C. V. Morton	*Thelypteris confluens* (Thunb.) Morton
5.	*Thelypteris crassifolia* (Blume) Ching	*Mesophlebion crassifolium* (Blume) Holttum
6.	*Thelypteris crinipes* (Hook.) K. Iwats.	*Christella crinipes* (Hook.) Holttum, B. Nayar & Kaur
7.	*Thelypteris dentate* (Forsskal) St. John	*Christella dentata* (Forsskal) Brownsey & Jermy
8.	*Thelypteris falciloba* (Hook.) Ching	*Pseudocyclosorus falcilobus* (Hook.) Ching
9.	*Thelypteris ferox* (Blume) Tagawa & K. Iwats.	*Chingia ferox* (Blume) Holttum
10.	*Thelypteri flaccida* (Blume) Ching	*Metathelypteris flaccida* (Blume) Ching
11.	*Thelypteris hirsutipes* (Clarke) Ching	*Coryphopteris hirsutipes* (Clarke) Holttum
12.	*Thelypteris hirtisora* (C. Chr.) K. Iwats.	*Sphaerostephanos hirtisorus* (C. Chr.) Holttum
13.	*Thelypteris interrupta* (Willd.) K. Iwats.	*Cyclosorus interruptus* (Willd.) H. Ito
14.	*Thelypteris larutensis* (Bedd.) Tagawa & K. Iwats.	*Sphaerostephanos larutensis* (Bedd.) C. Chr.
15.	*Thelypteris megaphylla* (Mett.) K. Iwats.	*Sphaerostephanos penniger* (Hook.) Holttum
16.	*Thelypteris nudata* (Roxb.) Morton	*Pronephrium nudatum* (Roxb.) Holttum
17.	*Thelypteris polycarpa* (Blume) K. Iwats.	*Sphaerostephanos polycarpus* (Blume) Copel.
18.	*Thelypteris repanda* (Fée) Tagawa & K. Iwats.	*Pronephrium repandum* (Fée) Holttum
19.	*Thelypteris siamensis* Tagawa & K. Iwats.	*Christella siamensis* (Tagawa & K. Iwats.) Holttum
20.	*Thelypteris singalanensis* (Baker) Ching	*Metathelypteris singalanensis* (Baker) Ching
21.	*Thelypteris sumatrana* (v.A.v.Ros.) K. Iwats.	*Pseudophegopteris sumatrana* Holttum
22.	*Thelypteris terminans* (Hook.) Tagawa & K. Iwats.	*Amphineuron terminans* (Hook.) Holttum
23.	*Thelypteris torresiana* (Gaud.) Alston	*Macrothelypteris torresiana* (Gaud.) Ching
24.	*Thelypteris truncata* (Poiret) K. Iwats.	*Pneumatopteris truncata* (Poiret) Holttum
25.	*Thelypteris viscose* (Baker) Ching	*Coryphopteris viscosa* (Baker) Holttum
26.	*Thelypteris xylodes* (Kunze) Ching	*Pseudocyclosorus xylodes* (Kunze) Ching
27.	*Thelypteris* sp.	*Trigonospora* sp.

2. *Character measurements*

In total, 21 quantitative and 11 qualitative characters of the collected specimens were studied and selected for multivariate analyses (Table 2-3). Measurements of morphological characters were carried out on fertile fronds. Measurements of macroscopic characters were performed using a standard ruler or a digital caliper, while microscopic characters were measured with the aid of a light microscope equipped with a 10X lens coupled to a micrometer disc and 10X or 40X objectives.

3. *Data analyses*

Cluster analyses (CA) and Canonical discriminant analysis (CDA) were performed to determine the pattern of grouping of the collected specimens (OTUs).

In cluster analysis when only quantitative characters were used, the original data matrix were standardized (STAND) and the resultant matrix was used to produce the distance matrix based on average taxonomic distance (DIST). Then, cluster analysis was conducted using the unweighted pair-group method arithmetic (UPGMA) in SAHN. These procedures are available in NTSYS-pc version 2.11S (Exeter Software © 2002 by Applied Biostatistics, Inc.).

When mixed characters, i.e. quantitative and qualitative morphological characters, were measured altogether, the Gower similarity coefficient was calculated and clustered by the group-average method as suggested by Gower (1971). For these proposes, a statistic package, MVSP (Kovach Computing Services, MVSP Plus, version 3.1) was used.

Canonical discriminant analysis was performed with SPSS 11.0 for Windows (SPSS Inc., Chicago, IL, USA). Stepwise discriminant analysis was used to select a subset of characters that maximized differences among the groups determined by clusters analysis. Correct classification rates were used as indicators of separation among the groups.

Table 2. Twenty one quantitative characters of fertile frond used in multivariate analyses of *Thelypteris* s.l. with their methods of scoring.

No.	Character	Details of measurements and counts
1.	scale width (mm)	width of scale at base of stipe
2.	scale length (mm)	length of scale at base of stipe
3.	stipe length (mm)	length of stipe
4.	rachis length (cm)	length of rachis
5.	basal pinnae width (cm)	width of basal pinnae
6.	basal pinnae length (cm)	length of basal pinnae
7.	angle of basal pinnae to rachis	-
8.	number of pinnae/frond	-
9.	distance between the pair of the largest pinnae (cm)	-
10.	lateral pinnae width (cm)	width of the largest lateral pinnae
11.	lateral pinnae length (cm)	length of the largest lateral pinnae
12.	pinnae lobe depth (mm)	perpendicular distance between margin and base of lobe
13.	number of sori per lobe	number of sori per lobe of the largest lateral pinnae
14.	lateral vein length (cm)	length of lateral vein of the largest lateral pinnae
15.	pair number of lateral veins/pinnae	-
16.	sporangium width (mm)	the longest distance measured from side to side of sporangium at the equatorial axis
17.	sporangium length (mm)	the longest distance measured from base to top of sporangium (without stalk)
18.	number of annulus cell	number of annulus cell/ sporangium
19.	stalk length (mm)	length of sporangium stalk
20.	spore height (mm)	height of spore from lateral view
21.	spore diameter (mm)	diameter of spore from lateral view

Table 3. Eleven qualitative characters of fertile frond used in multivariate analyses of *Thelypteris* s.l. with their methods of scoring.

No.	Character	Details of measurements and counts
1.	form of rhizome	erect (1), suberect (2), short creeping (3), long creeping (4)
2.	buds on rachis	absent (0), present (1)
3.	basal pinnae	not or slightly reduced (1), extremely reduced (2), suddenly reduced to form butterfly shaped auricles (3)
4.	form of frond	once-pinnate (1), bi-pinnate-tri-pinnatifid (2)
5.	upper-surface of costae	not grooved (0), grooved (1)
6.	margin of pinnae	subentire (1), pinnae lobed less than half way to costae (2), pinnae lobed to half way towards costae (3), pinnae always deeply lobed (4)
7.	venation pattern	vein free (1), vein anastomosing (2), vein in several pairs all anastomosing and joining to form zigzag composite vein alternating with the costules (3)
8.	Sori	exindusiate (0), indusiate (1)
9.	acicular hairs or glandular hairs on sporangium	absent (0), present (1)
10.	acicular hairs or glandular hairs on sporangium stalk	absent (0), present (1)
11.	spore type	monolete (1), trilete (2)

Results and Discussion

1. *Cluster analysis*

In cluster analysis, two similarity (or distance) coefficient matrices were produced. The first matrix was the average taxonomic distance derived from 21 quantitative characters and the second one was the Gower's similarity coefficient matrix derived from 21 quantitative characters plus 11 qualitative characters.

The results of the first cluster analysis using the average taxonomic distance matrix is shown in Figure 1. The dendrogram split the 518 specimens into three groups (Group A-C) using an average taxonomic distance of 1.50. The first group (A) consisted of twenty three species (*Meniscium proliferum, Thelypteris arida, T. ciliata, T. confluens, T. classifolia, T. crinipes, T. dentata, T. falciloba, T. ferox, T. flaccida, T. hirsutipes, T. hirtisora, T. interrupta, T. larutensis, T. megaphylla, T. polycarpa, T. siamensis, T. singalanensis, T. terminans, T. truncata, T. viscosa, T. xylodes, T.* sp.). The second group (B) comprised two taxa, namely *T. torresiana* and *T. sumatrana*, whilst the third group (C) included two species: *T. nudata* and *T. repanda*.

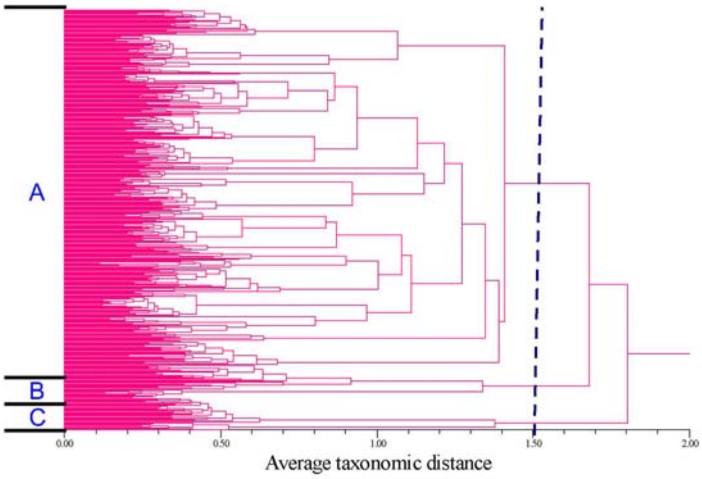

Figure 1. UPGMA clustering of 518 OTUs based on 21 characters of *Thelypteris* s. l. in Thailand.

Similar results were obtained when both quantitative and qualitative characters were used. The dendrogram derived from the second cluster analysis is shown in Figure 2. Using the 70% similarity phenon line as a reference (Sneath and Sokal, 1973), three main groups could be distinguished in the UPGMA phenogram. Members of the three groups (Group A-C) were the same as those of the three groups obtained from the first cluster analysis.

In group A, there were 13 genera according to Holttum's classification (1971 and 1981). They are *Ampelopteris, Amphineuron, Chingia, Christella, Coryphopteris, Cyclosorus, Metathelypteris, Mesophlebion, Pneumatopteris, Pseudocyclosorus, Sphaerostephanos, Thelypteris* and *Trigonospora*. Holttum (1971, 1981) used a combination of characters to distinguish the 13 mentioned genera. In contrast, according to Tagawa and Iwatsuki (1988), 23 species of group A were subdivided into 22 species of *Thelypteris* and one species of *Meniscium* (Table 1). They used a proliferous character of the rachis to separate *Meniscium* from *Thelypteris*.

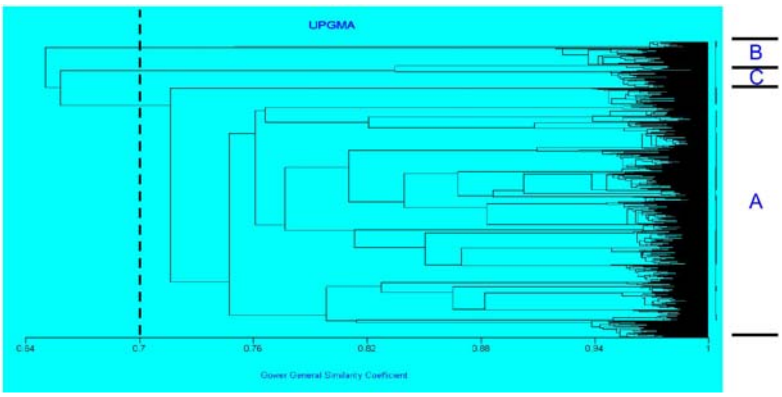

Figure 2. UPGMA phenogram base on Gower's general similarity coefficient calculated between means of 21 quantitative and 11 qualitative morphological characters of the genus *Thelypteris* s.l. in Thailand.

In the light of both cluster analyses, it is evident that group A should be sorted only into one genus/taxon, preferably grouped into the genus *Thelypteris* since the type genus "*Thelypteris*" is in this cluster and this taxon has higher priority than the others.

A close examination of the dendrogram in Figure 2 reveals that two subclusters could be established. Subcluster 1 comprised *T. prolifera*, corresponding to *Ampelopteris* sensu Holttum or *Meniscium* sensu Tagawa and Iwatsuki. It is noteworthy that both authors used the same characters to classify this taxon, i.e. proliferous character on the rachis. The other cluster contained the remaining 12 genera as mentioned earlier.

Two taxa in group B conformed to the genera *Pseudophegopteris* and *Macrothelypteris* according to Holttum's classification (1971). Holttum recognized these two genera based on characters of scales on fronds and spore morphology. However, Pichi Sermolli (1970) recognized only one genus, and transferred all species of *Pseudophegopteris* to *Macrothelypteris*. Unification of these two genera was based on bi-pinnate fronds. It is evident that the results of cluster analyses from this study support Pichi Sermolli's classification.

All OTUs in group C were members of the genus *Pronephrium* sensu Holttum. Holttum (1971) used venation pattern as an important character to separate the genus *Pronephrium* from the other genera in his classification. He noted that when pinnae lobes are not deep, veins from adjacent costules joined to form an excurrent straight or zigzag vein. These united veins run to the translucent membrane at the base of a sinus between two lobes (Holttum, 1971). It can be seen that the results of cluster analyses clearly supports the separation of the genus *Pronephrium* from the majority of *Thelypteris* s.l.

In all, the results of cluster analyses supported the recognition of the three genera, i.e., *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium*.

2. Canonical discriminant analysis

In canonical discriminant analysis, 21 characters were evaluated by stepwise discriminant analysis to determine which characters were important in discriminating among these three groups as suggested by cluster analyses. The following 19 out of 21 characters, 1, 2, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, and 21 were selected as important characters in giving the best separation of the groups (Table 4). In addition, the specimens were correctly classified into their respective groups (A, B, or C) with 100% accuracy. These classification rates are extremely high considering the existing variation among the three groups. The result was the same when the original group (27 taxa) was used as *a priori in canonical discriminant analysis*, i.e., yielding 3 groups in an ordination plot (Fig. 3).

The ordination plot of the 518 OTUs was presented on the two canonical axes (Fig. 3). It can be seen that group B is clearly separated from groups A and C on canonical axis 1. Likewise, group C is evidently separated from groups A and B on canonical axis 2. So, the three groups appear distinct. Canonical variable 1 (axis 1) is most highly influenced by five characters (Table 4), viz. scale width (1), angle of basal pinnae to rachis (7), number of annulus cells (18), spore height (20) and spore diameter (21). The canonical correlation of the

Table 4. Pooled within canonical structure of 3 groups/taxa (A-C) according to the result of canonical discriminant analysis.

Character	Axis 1	Axis 2
1. scale width	-0.018*	0.004
2. scale length	0.022	0.053*
3. stipe length [a]	-0.026	0.165*
4. rachis length	-0.020	0.081*
5. basal pinnae width	0.306	0.448*
6. basal pinnae length	0.064	0.243*
7. angle of basal pinnae to rachis	0.038*	0.020
8. number of pinnae/frond [a]	-0.003	-0.106*
9. distance between the pair of the largest pinnae	0.015	0.190*
10. lateral pinnae width	0.269	0.428*
11. lateral pinnae length	0.025	0.154*
12. pinnae lobe depth	0.081	-0.171*
13. number of sori per lobe	-0.156	0.232*
14. lateral vein length	-0.086	0.349*
15. pair number of lateral veins/ pinnae	-0.114	0.228*
16. sporangium width	0.067	-0.187*
17. sporangium length	0.050	-0.210*
18. number of annulus cell	0.075*	0.019
19. stalk length	0.004	-0.094*
20. spore height	0.042*	-0.020
21. spore diameter	0.099*	0.076

***** Largest absolute correlation between each variable and any discriminant function
a This variable not used in the analysis

first canonical discriminant function is 98% with all the variables and the variance explained by it is 77%. Thus, these two axes are effective for separating the three morphological groups of the genus *Thelypteris* s.l. in Thailand.

From the ordination plot in Figure 3, it can be seen that, among the three groups, group B was rather heterogeneous, while group C and group A were less variable in descending order of variation.

It can be concluded that cluster analyses and canonical discriminant analyses from this study do not support a separation of *Thelypteris* s.l. in Thailand into neither the two genera proposed by Tagawa and Iwatsuki (1988), nor the 16 genera (Table 1) according to Holttum's classification (1971, 1981). In contrast, the results from this study do support the separation of *Thelypteris* s.l. in Thailand into 3 genera, i.e. *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium* based on both quantitative and qualitative characters. Corresponding results were presented by Smith and Cranfill (2002), they recognized 5 genera, namely *Macrothelypteris, Pseudophegopteris, Phegopteris*, *Thelypteris* s.s. and *Cyclosorus* sensu Smith based on data from four chloroplast genes (*rps*4 gene + *rbc*L gene + *trn*S spacer, + *trn*L spacer; 2,600 base pairs) of specimens from 23 genera according to Holttum's classification. They noted that their sampling was as yet insufficient to favor one classification over another. It is pertinent to note that the present analysis suggested that recognition of an intermediate number of genera may be the most suitable for classification in the Thelypteridaceae.

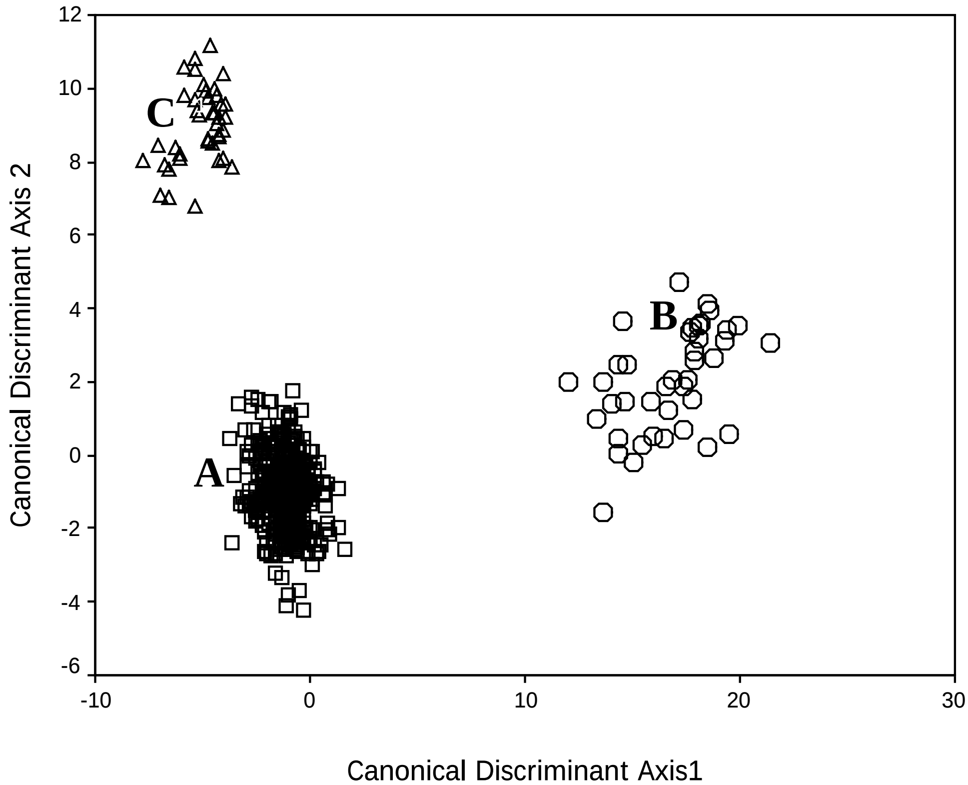

Figure 3. Ordination plot of 518 specimens from 27 taxa of *Thelypteris* s.l. in Thailand based on 21 quantitative characters.

3. Important characters

Univariate analysis of 21 quantitative characters was performed (Table 5). It can be seen that there were statistical significant differences ($P<0.05$) in all characters among the three proposed genera, viz. *Thelypteris*, *Macrothelypteris* and *Pronephrium*. The F-values (Table 5) indicate by their magnitude the relative order of importance of the characters in general. It is clear that the F-values almost reflect the association of characters with canonical axis 1 because of its high correlation and high explained variance. Basic statistics for the three proposed genera are summarized in Table 5. It can be concluded that the vegetative characters of *Thelypteris* s.s. and *Pronephrium* were generally larger than those of *Macrothelypteris.* In contrast, the reproductive characters of *Macrothelypteris* were larger than those of *Thelypteris* and *Pronephrium*.

Table 5. F-values, means and standard errors of 21 quantitative characters of the three genera

No.	Character	F-value	Sign.	*Thelypteris* s.s.		*Macrothelypteris*		*Pronephrium*	
				mean	± SE	mean	± SE	mean	± SE
1	scale width	3.406	0.034	0.989	0.022	0.802	0.012	0.987	0.029
2	scale length	4.653	0.010	7.122	0.220	8.938	0.288	8.463	0.341
3	stipe length	64.369	0.000	34.694	1.052	42.962	2.127	73.290	1.419
4	rachis length	12.643	0.000	78.026	3.116	62.292	1.407	125.337	8.030
5	basal pinnae width	1389.034	0.000	1.209	0.025	8.205	0.379	3.647	0.071
6	basal pinnae length	180.645	0.000	6.951	0.340	21.170	0.974	24.115	0.473
7	angle of basal pinnae to rachis	9.105	0.000	109.431	41.786	136.250	0.557	107.000	1.761
8	basal pinnae length	180.645	0.000	6.951	0.340	21.170	0.974	24.115	0.473
9	angle of basal pinnae to rachis	9.105	0.000	109.431	41.786	136.250	0.557	107.000	1.761
10	lateral pinnae width	1086.859	0.000	1.683	0.035	8.402	0.348	4.455	0.065
11	lateral pinnae length	50.752	0.000	14.984	0.430	22.202	0.890	27.727	0.601
12	pinnae lobe depth	78.586	0.000	4.015	0.086	5.597	0.095	1.051	0.032
13	number of sori per lobe	358.855	0.000	10.774	0.241	3.175	0.607	30.700	0.782
14	lateral vein length	373.739	0.000	0.861	0.017	0.700	0.018	2.416	0.059
15	pair number of lateral veins/ pinnae	241.801	0.000	35.641	0.766	17.325	0.430	84.775	0.844
16	sporangium width	80.274	0.000	0.192	0.001	0.213	0.001	0.130	0.008
17	sporangium length	74.180	0.000	0.243	0.002	0.253	0.001	0.155	0.012
18	number of annulus cell	37.463	0.000	15.016	0.078	17.275	0.277	14.800	0.130
19	stalk length	17.531	0.000	0.189	0.003	0.175	0.011	0.121	0.007
20	spore height	13.198	0.000	0.030	0.000	0.033	0.001	0.028	0.000
21	spore diameter	81.385	0.000	0.041	0.000	0.052	0.001	0.043	0.000

Conclusions

Thelypteris s.l. is a large and complex genus comprising about 1,000 species and has been a single genus in the family Thelypteridaceae (Vasudeva and Bir, 1993), since its separation from the dryopteroid ferns about 60 years ago. Although generally recognized as a natural monophyletic group, there are still some differences in opinion among pteridologists on generic circumscription.

This study was focused on numerical taxonomy. 518 specimens (OTUs) from 27 species of *Thelypteris* s.l. in Thailand were subjected to cluster analyses and canonical discriminant analysis. Based on 21 quantitative characters and supported by 11 qualitative characters, cluster analysis strongly indicated the presence of three distinct groups, i.e. *Thelypteris* s.s., *Macrothelypteris* and *Pronephrium*. The 3 groups were subsequently evaluated by canonical discriminant analyses. It was found that 5 characters, i.e. scale width, angle of basal pinnae to rachis, number of annulus cells, spore height and spore diameter collectively supported the segregation of 3 groups or genera from the *Thelypteris* s.l.

The following is an identification key to the genera segregated from the *Thelypteris* s.l. in Thailand.

1a Frond 2-3 pinnate; number of annulus cells equal to or more than 17…... 1. *Macrothelypteris*

1b Frond 1-pinnate; number of annulus cells less than 17

2a Spore diameter less than 0.43 mm …………………………………… 2. *Thelypteris*

2b Spore diameter equal to or more than 0.43 mm .... 3. *Pronephrium*

In all, numerical taxonomy can re-examine the principles of taxonomy, especially the proposed classification. This computerized processing technique has proven useful for the classification of *Thelypteris* s.l. in Thailand.

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